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ARTICLE

Does the Lunar Cycle Affect Reef Fish Catch Rates?

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Abstract
The lunar cycle was examined as a potential source of variation in CPUE for the most common commercial reef fish species captured in the Gulf of Mexico. Using fishery observer data for species captured with bottom longline and vertical line gear types, the analyses modeled CPUE with two different approaches: (1) a generalized additive model with cyclic splines to explain nonlinear variations with the 29.5-d lunar cycle; and (2) a generalized linear model using periodic regression with the sine and cosine functions to describe cyclic variations in CPUE. A lunar effect on catch rates was detected for Red Grouper *Epinephelus morio* and Tilefish *Lopholatilus chamaeleonticeps*; however, no lunar effect was detected for Yellowedge Grouper *Hyporthodus flavolimbatus*, Red Snapper *Lutjanus campechanus*, or Vermilion Snapper *Rhomboplites aurorubens* based on either method. The lunar effect in the bottom longline fishery differed between species, with increased CPUE consistently predicted to occur near the new moon for Red Grouper and to take place proximal to the full moon for Tilefish. Red Grouper captured with vertical line gear had two CPUE increases predicted around the waxing and waning lunar phases. Inconsistencies in lunar effect between gear types for Red Grouper were present, possibly due to different mechanisms affecting CPUE. Results suggest that lunar cycles influence catch rates for some of the reef fish species examined and should be considered as potential environmental covariates for standardizing nominal CPUE.

Environmental changes from the lunar cycle, circadian rhythm, or seasonal and tidal patterns have long been thought to influence the behavior of marine life. One recent examination of the lunar and tidal cycles found evidence that they synchronize activity on the cellular level across a wide variety of marine species (Tessmar-Raible et al. 2011). Of particular interest to recreational fishers is the use of "Solunar" tables to predict periods of increased fish activity related to the sun and moon. This Solunar theory, developed by John Knight in 1926, uses a combination of lunar, tidal, and solar information to predict when fish are more likely to be active and thus more likely to be captured (Florida FWC 2016). Knight attempted to validate his theory by comparing "record" catches, finding that 90% of such catches occurred during a new moon.

More recently, scientific studies examining the effect of the lunar cycle on catch rates have realized a varying degree of influence depending on the species, fishery, sample size, and statistical methodology. Using periodic regression, Vinson and Angradi (2014) found that catch rates of Muskellunge *Esox masquinongy* were strongly influenced by the 29.5-d lunar cycle, with catch rates increasing by a maximum of about 5% near the new and full moons. Those authors proposed that the ability to detect a lunar influence outside of variability linked to other factors affecting Muskellunge catchability increased due to their analysis of a large data set, with 341,959 catch records spanning a 40-year period and a broad geographic range. In a separate analysis of recreational data with periodic regression, Lowry et al. (2007) determined that the lunar cycle was correlated with differences in catch rates for five of eight pelagic finfish or shark species examined in Australia. The study by Lowry et al. (2007) found interspecific differences in predicted lunar effects, but for most species, increased catch rates were predicted to occur proximal to the new moon. Similarly using a large data set with pelagic finfish species, significant lunar effects on catch rates were detected in a study of the commercial fishery for Albacore *Thunnus alalunga* and Swordfish *Xiphias gladius* in the Reunion Islands (Poisson et al. 2010). Catch rates for the two species

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increased at different times, with Albacore CPUE increasing during the full moon and Swordfish CPUE increasing during the first and last quarters. Using a generalized additive model (GAM), Ortega-Garcia et al. (2008) found that lunar phase explained a small (<1%) but significant amount of variation in the catch rates of Striped Marlin *Kajikia audax* for sportfishing vessels operating out of Mexico. Although the small lunar effect on catch rates identified by Ortega-Garcia et al. (2008) is consistent with other studies of similar species, their research may have been limited since the vessels fished in different daily durations that were not recorded to standardize effort. These studies proposed different mechanisms, such as shifts in predator–prey dynamics, altered vertical migration patterns, light level differences, and other behavioral changes, to explain the differences in catch rates during the lunar cycle.

The commercial fishery for reef fish in the Gulf of Mexico (hereafter, "Gulf") primarily targets grouper (family Serranidae) and snapper (family Lutjanidae) species by using bottom longline and vertical line gear. Many of these economically important reef fish species share a number of traits, such as slow growth, high site fidelity, complex social structures, and predictable spawning aggregations that make them susceptible to overexploitation (Coleman et al. 2000). Most of the targeted species are opportunistic, predatory feeders, with groupers generally employing a sedentary foraging strategy that involves lying in wait and ambushing their prey (Thompson and Munro 1978). Only two studies could be identified that examine how the lunar cycle affects catch rates for primarily reef-dwelling finfish species captured by hook and line (Millar et al. 1997; Stevenson and Millar 2013). Stevenson and Millar (2013) determined that the lunar cycle significantly affected CPUE for a reef species, the Silver Seabream *Pagrus auratus*, in New Zealand. Although Stevenson and Millar (2013) found that the highest catch rates occurred just after the new moon, the effect size was relatively small, with at most a 13.7% difference in Silver Seabream catch rates when comparing the most and least favorable days in the lunar cycle.

The purpose of the present study was to determine whether the lunar cycle was related to catch rates for the most common species of reef fish captured in the commercial fishery within U.S. waters of the Gulf. For bottom longline gear, the three most common targeted species examined were the Red Grouper *Epinephelus morio*, Yellowedge Grouper *Hyporthodus flavolimbatus*, and Tilefish *Lopholatilus chamaeleonticeps*, which collectively accounted for over 74% of all captures observed. The three most common species targeted in the vertical line fishery were the Vermilion Snapper *Rhomboplites aurorubens*, Red Snapper *Lutjanus campechanus*, and Red Grouper, which together comprised over 52% of total captures. Beyond the basic interest in effects of lunar activity on reef fish behavior, lunar information could improve current models for standardizing CPUE for any of these species if it is discovered to significantly affect the efficiency of baited fishing gear. Inclusion of such environmental information could improve time-series indices of abundance for managers when evaluating long-term population trends. To determine lunar effects on catch rates, two different approaches were used: (1) a GAM with cyclic splines to explain nonlinear variation in CPUE with the 29.5-d lunar month; and (2) a generalized linear model (GLM) using periodic regression with sine and cosine functions to explain cyclic variations in CPUE.

METHODS

Background and data preparation.—The data set used in the study encompassed fishery-dependent catch information collected during July 2006–December 2015 by the Reef Fish Observer Program of the National Marine Fisheries Service's Galveston Laboratory; the data set included the frequency of kept and discarded species for each individual fishing set (NMFS 2016). For the mandatory Reef Fish Observer Program in the Gulf, commercial fishing vessels were randomly selected quarterly each year to carry an observer. Sampling effort was stratified by season and gear in the eastern and western Gulf based on annually updated vessel logbook data (Scott-Denton et al. 2011). Beginning in February 2009, increased observer coverage levels were directed at the bottom longline fishery in the eastern Gulf due to concerns regarding sea turtle interactions. Additionally, in 2011, increased funding allowed for enhanced coverage of both the vertical line and bottom longline fisheries through 2014. Because of these actions, observer coverage levels did not remain consistent throughout the years (<1% to ~5%) but instead varied depending on funding levels. Despite these variations in coverage level, catch data were collected from vessels using multiple gear types across broad spatial and temporal scales that were representative of the fishery. The frequency of fish captures during each fishing set was standardized into a catch rate by including the number of hooks sampled during fishing sets as an offset in both the GAM and GLM approaches. For bottom longline gear, the number of hooks sampled was determined by counting the number of baited hooks that were deployed. In the vertical line fishery, the number of hooks sampled was the summation of baited hooks dropped to a fishing depth at unique locations. Catch rates could not be calculated from the bottom longline fishery data prior to 2010 because an accurate count of the hooks sampled was not recorded during those years. Since the catch composition was dominated by relatively few species, the decision was made to examine the potential lunar effect for the three most common species targeted by each gear type in addition to the total number of all species captured (total catch) during individual fishing sets. Using the criteria already specified, catch information from 7,520 bottom longline sets and 37,247 vertical line sets were available for the analyses (Table 1). All analyses in this research were performed using R version 3.3.0 (R Development Core Team 2016).

Lunar information was matched to the existing catch data as a continuous variable by using the "lunar" package available in R software (Lazaridis 2014). The default continuous lunar variable returned from the lunar package was expressed in radians and was converted to the 29.5-d synodic lunar month beginning with the new moon by using the equation

$$\text{Lunar Day} = \text{Lunar Radians} \times 3\pi/2. \tag{1}$$

Lunar information matched to the data set was cross-referenced against data from the U.S. Naval Observatory's Astronomical Information Center to ensure accuracy (U.S. Naval Observatory 2016). Data were examined for evidence of skewed effort (fishing sets) during the lunar cycle when examining histograms of each data set for deviation from a uniform distribution (Supplementary Figures S.1–S.3 available in the online version of this article). The histograms did indicate more effort during the waning moon phase for the bottom longline gear type, most notably for Tilefish; however, effort was still present throughout the entire lunar cycle. Initial data exploration indicated that overdispersion and zero inflation were present for some of the species of interest, particularly those captured by vertical line gear. A large proportion of the zero inflation could be explained by the fishing vessels targeting other species of interest and did not represent a true-zero CPUE observation, as no target fish of interest would be expected during those fishing sets. The solution was to truncate the datum for each species to fishing sets for which that species of interest was recorded as one of the primary target species during the set. Beginning in late 2008, the observer program began recording up to three different primary target species, as indicated by the captain, for individual fishing sets. Vertical line data prior to late 2008 that lacked target species information were excluded from the analyses for individual species of interest but were included in the total catch analysis.

In addition to the lunar cycle, other variables were included as random covariates since they could confound or obscure the lunar effect. Besides differences in gear type, the covariates of year, month, depth, area, and time of day were available for both modeling approaches and were included in the final models regardless of significance. Year was included due to potential fluctuations in population abundance over the study period. Month was derived from the capture date to account for catchability differences possibly related to temperature or spawning periods. Depth of capture (m) was also included since size distributions for some of the species of interest may have differed across depth strata. Instead of latitude or longitude, area was included as a categorical variable in the models using statistical zones (NMFS 2016) because for some subsets of the data, collinearity was detected between latitude or longitude and depth. When a model for a given species failed to converge due to limited observations in certain regions, the statistical zones were aggregated to represent the following regions: 1–3 (Florida Keys), 4–7 (west Florida), 8–9 (northwest Florida), 10–12 (Alabama/Mississippi), 13–17 (Louisiana), and 18–21 (Texas). Box plot summaries of the lunar cycles by year and month for each gear type determined that no outliers or skewed distributions were present, except for a lack of data around the new moon for vertical line gear in 2006.

The start time was available for fishing sets using both gear types and was converted into a categorical variable since effort was highly skewed toward daylight hours (Figure S.4). The start times were converted into the following categories: 0600–1000 hours (morning), 1001–1600 hours (mid-day), 1601–2000 hours (evening), and 2001–0559 hours (night). The category ranges attempted to account for differences that may have been present in catch rates proximal to the sunrise or sunset. Unique vessel identification was considered as a possible random effect, but many vessels changed owners,

TABLE 1. Number of captures and targeted fishing sets for the three most common species and total catch for each gear type used in the commercial fishery for reef fish in the Gulf of Mexico.

Species	Number of target captures observed	Number of target fishing sets	Mean hooks fished per set	Mean CPUE (catch per 1,000 hooks)
		Bottom longline		
Red Grouper	271,978	5,866	648.8	73.06
Yellowedge Grouper	20,732	1,386	770.8	20.61
Tilefish	19,104	487	781.3	55.43
Total catch (all species)	418,169	7,520	647.7	85.15
		Vertical line		
Vermilion Snapper	106,359	8,144	117.8	77.57
Red Snapper	74,191	7,049	68.41	123.83
Red Grouper	72,225	22,312	26.27	139.94
Total catch (all species)	485,125	37,247	49.83	229.76

captains, or both during the study period, thus making vessel identification problematic. The observer program began recording bait type for individual fishing sets in 2009; however, inferences based on bait type were not possible since multiple bait types were recorded on almost all fishing sets, but the proportion of hooks baited with each bait type was not recorded.

Generalized additive modeling.—The first statistical modeling approach for examining the differences in catch rate was a GAM with cyclic splines representing the 29.5-d lunar cycle as a continuous covariate and with year as a categorical variable. Originally, both negative binomial and a zero-inflated Poisson distributions were chosen to examine the possible lunar effect using a GAM; however, all exploratory models had a substantially better fit using the negative binomial distribution, as evidenced by large (>25%) decreases in Akaike's information criterion (AIC; Akaike 1974). The decision was then made to use only the negative binomial distribution to model the catch rates of the three species of interest and the total catch for each gear type. The decision was supported by a recent study by Drexler and Ainsworth (2013), who found that GAMs using a negative binomial distribution were suitable for modeling similar fishery data sets containing excessive zeroes. All GAMs were fitted with the "mgcv" package in R with the following equation using a spline (s) for the lunar effect and a log link function (Wood 2011),

$$\text{Number Captured} \sim s(\text{Lunar Day}) + \text{Year} + \text{Month} + \text{Depth} + \text{Area} + \text{Time of Day} + \text{offset}[\log_e(\text{Hooks Sampled})]. \tag{2}$$

The smoothing dimension or number of knots (k) for the cyclic lunar effect was increased if necessary so that it was not restrictively low using the "gam.check" function in the mgcv package to compare k to the estimated degrees of freedom. The approximate significance of the smoothing parameter for the lunar effect, percent of deviance explained, and adjusted R^2 were reported by using the summary function for each model. The change in AIC obtained by including the lunar spline was calculated by comparing nested models with the spline removed. Model validation included (1) examining the quantile–quantile (Q–Q) plots of reference quantiles with simulated deviance residuals, Q–Q plots of reference quantiles with Pearson residuals, and histograms of the Pearson residuals; (2) checking the Pearson residuals against the fitted values for violations of constant variance; and (3) comparing the fitted versus observed values. For each gear type, a bar plot of the mean observed CPUE for each day in the 29.5-d lunar cycle was compared to the predicted GAM fit with 95% confidence intervals. Finally, the exponentiated smoothed curves of the additive lunar effect on predicted CPUE were compared between species and between gear types.

Periodic regression generalized linear modeling.—The second analysis approach examined the use of periodic regression to explain lunar variations in CPUE via the protocol proposed by deBruyn and Meeuwig (2001). Those authors found that periodic regression had greater statistical power in detecting a lunar effect relative to a categorical ANOVA using simulated and actual data sets. Their study used ordinary least-squares (OLS) regression with a sine or cosine function to explain cyclic variation in CPUE, treating the lunar cycle as a continuous covariate in radians (θ), an angular unit of lunar measurement. Since some catch rates in this study contained zero inflation and overdispersion, log transformation or root–root transformation to normalize the data for OLS regression would likely have been problematic. Therefore, a GLM with a negative binomial distribution was chosen to model the data using periodic regression. When modeling CPUE with Alaskan fishery observer data, Mateo and Hanselman (2014) recommended dismissing GLMs outright in favor of GAMs when nonlinearity of important covariates is present. However, it was decided that comparing multiple modeling approaches on the same data sets might provide insights into the resolution for detecting a potential cyclic lunar effect and that the corresponding models could be compared using AIC.

The periodic regression GLMs were fitted by using the "glm.nb" function in the R package MASS (Venables and Ripley 2002). The following equation was used to model the lunar effect, once again including random effects, hooks sampled as an offset, and a log link function:

$$\text{Number Captured} \sim \sin\theta + \cos\theta + \sin 2\theta + \cos 2\theta + \text{Year} + \text{Month} + \text{Depth} + \text{Area} + \text{Time of Day} + \text{offset}[\log_e(\text{Hooks Sampled})]. \tag{3}$$

The cosine terms represent a shift at 0° or 180°, corresponding with the new and full moons, respectively; and the sine terms represent a shift at 90° or 270°, corresponding to the waxing and waning lunar phases, respectively. Initially, all models were fitted using both θ (to describe a single phase shift and change in amplitude during the lunar cycle) and 2θ (to explore evidence of a semilunar cycle; i.e., two peaks per lunar month). Stepwise backward regression was used to remove nonsignificant ($P >$ 0.05) cyclic terms (sine or cosine) until only significant cyclic terms remained. As previously described, random factors were included in the final model regardless of its significance, and significant cyclic terms were reported using the χ^2 test on the difference of log likelihoods. For all significant cyclic terms in each final model, the exponentiated coefficient with 95% confidence intervals were generated using the "confint" function. Overall model goodness of fit was evaluated by using the χ^2 test with the residual deviance and the degrees of freedom equal to the residual degrees of freedom of the model. Model validation also included (1) plotting the deviance residuals versus the fitted values, (2) creating *Q*–*Q* plots of the standardized deviance residuals, (3) determining the presence of outliers, and (4) performing a Shapiro–-Wilk test for the normality of deviance residuals. Each final periodic regression GLM was compared to its corresponding GAM by using AIC.

RESULTS

The lunar cycle was a significant ($P < 0.05$) covariate with CPUE for five of the eight GAMs fitted to each datum (Table 2; Supplementary Tables S.1–S.4). The lunar cycle was not a significant covariate for Yellowedge Grouper ($P = 0.317$) captured with bottom longline gear, Vermilion Snapper ($P = 0.461$) captured with vertical line gear, or Red Snapper ($P = 0.463$) captured with vertical line gear. The percentage of deviance explained ranged from a minimum of 18.3% for bottom longline total catch to a maximum of 67.1% for vertical line total catch. Negative adjusted R^2 was reported for Red Grouper captured on vertical line gear, possibly due to the higher estimated degrees of freedom that were needed when fitting the splines. Values of AIC indicated that the lunar spline improved the fit (reduction > 2) of each model except those for the Yellowedge Grouper, Vermilion Snapper, and Red Snapper. The largest reduction in AIC from the lunar spline was for Red Grouper captured by both gear types. For the bottom longline fishery, the bar plot of the mean observed CPUE with the predicted GAM fitted for each day in the 29.5-d lunar cycle showed a good fit for each species (Figure 1). The smoothed curves of the additive lunar effect on predicted CPUE for bottom longline gear closely followed a cosine function for Red Grouper and for total catch, with maximum CPUE occurring near the new moon and lower catch rates predicted to occur close to the full moon (Figure 2). Red Grouper and all bottom longline captures had similar predicted smooth coefficient values, with approximately 1.05–1.10 times higher catch rates predicted near the new moon and 0.05 lower catch rates around the full moon. Tilefish had a predicted smooth coefficient value that was higher (~1.4) just prior to the full moon and an additional increase in catch rates predicted to occur near the waning lunar phase. All models had acceptable fit, as indicated by the diagnostic plots (Figures S.5–S.8).

The bar plot of the mean observed CPUE with the predicted GAM fitted for vertical line gear indicated a good fit for each species; however, more variation existed between days in the mean observed CPUE for the snapper species, with a large decrease in catch rates for Red Snapper occurring immediately after the full moon (Figure 3). The smoothed curves of the additive lunar effect on predicted CPUE for the vertical line fishery were not as consistent in predicting the lunar effect for multiple species (Figure 4). For the two most common vertical line species observed (i.e., Vermilion Snapper and Red Snapper), the GAMs only predicted slight changes in CPUE with the lunar cycle. Red Grouper and vertical line total catch had the largest significant increases in CPUE predicted to occur during the waning and waxing lunar phases, with decreases in CPUE proximal to the full moon and new moon.

Red Grouper had the largest predicted increase in catch rates for vertical line captures, with a smooth coefficient value of approximately 1.1 indicating higher catch during the waning lunar phase, preceded by a slightly smaller increase during the waxing lunar phase. Red Grouper and total captures with vertical line gear both had the smallest smooth coefficient values predicted to occur proximal to the new moon and full moon. The predicted changes in CPUE using the GAMs with the lunar cycle were inconsistent for the same species between gear types. For example, the highest CPUE for Red Grouper was predicted to occur near the new moon using bottom longline gear, but the lowest CPUE was predicted to take place near the new moon with vertical line gear. All GAMs

TABLE 2. Generalized additive model results from the three most common species and total catch for each gear type in the commercial fishery for reef fish in the Gulf of Mexico. The likelihood ratio *P*-value for the lunar spline, percentage of model deviance explained, model-adjusted R^2, and reduction in Akaike's information criterion (ΔAIC) from including the lunar spline (*s*[Lunar Day]) are reported.

Species	Lunar χ^2 *P*-value	Deviance explained (%)	Adjusted R^2	ΔAIC (*s*[Lunar Day])
		Bottom longline		
Red Grouper	<0.001	29.6	0.227	36.19
Yellowedge Grouper	0.317	25.0	0.267	–0.62
Tilefish	<0.001	63.4	0.02	13.82
Total catch (all species)	<0.001	18.3	0.189	31.96
		Vertical line		
Vermilion Snapper	0.461	41.7	0.539	–0.16
Red Snapper	0.463	53.5	0.726	0.18
Red Grouper	<0.001	40.0	–0.371	28.7
Total catch (all species)	<0.001	67.1	0.696	30.8

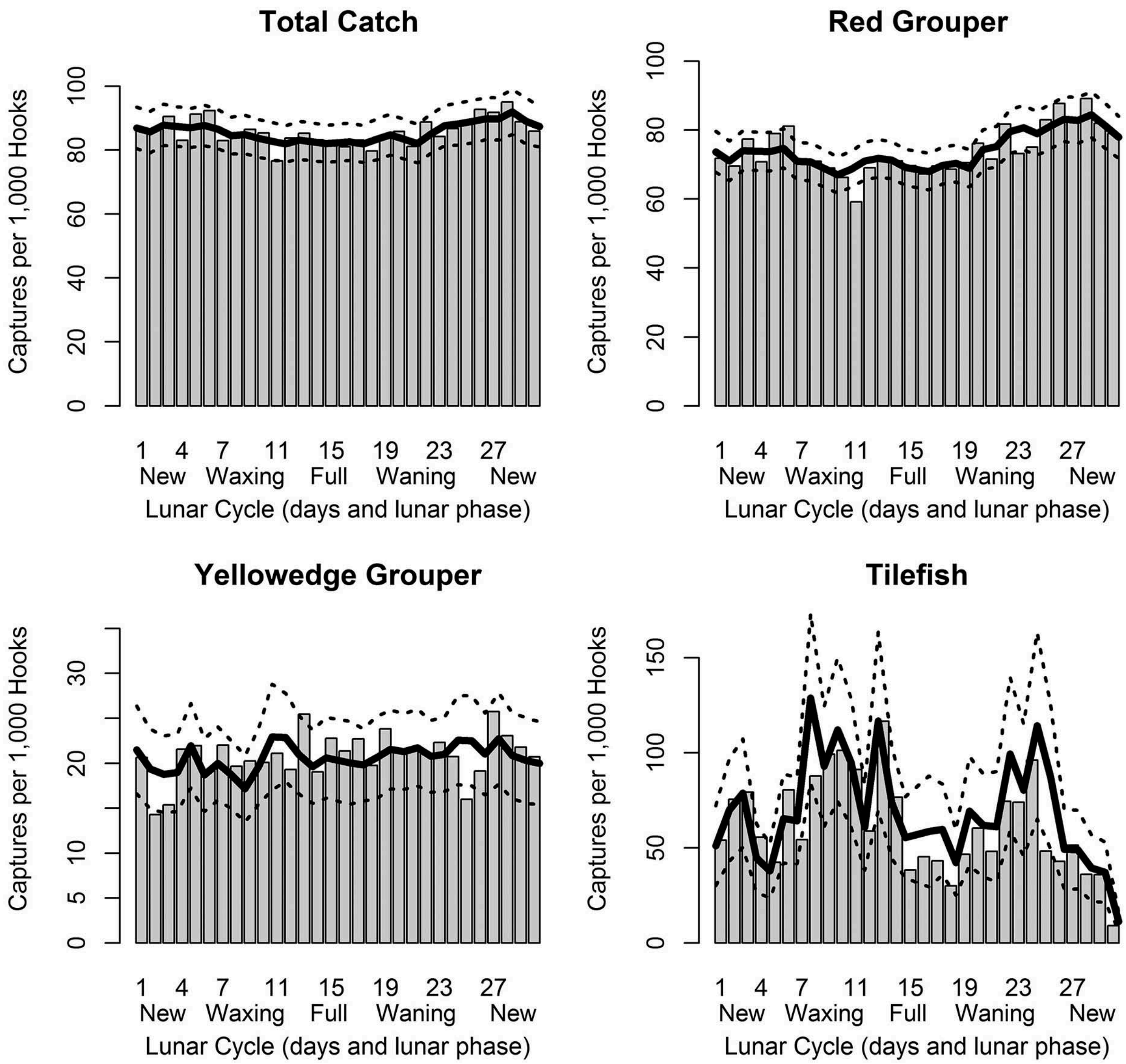

FIGURE 1. Bar plot of the mean observed CPUEs for each day in the 29.5-d lunar cycle compared with the CPUEs predicted by generalized additive models (solid line; ±95% confidence interval) for the three most common species and total catch with bottom longline gear based on data from the commercial fishery for reef fish in the Gulf of Mexico.

used for vertical line gear had acceptable fit, as indicated by the diagnostic plots, but a comparison of the residuals revealed that models fitted to bottom longline data generally provided a better fit than models fitted to vertical line data.

For the second modeling approach of periodic regression using GLMs, the results were consistent with each corresponding GAM. A significant sine or cosine term was fitted using backward regression for each species except the Yellowedge Grouper, Red Snapper, and Vermilion Snapper (Table 3). For Vermilion Snapper, a model could not be successfully fitted due to a lack of convergence with the software, thus preventing any inference on cyclic terms for that species. Multiple cyclic terms were significant for the Tilefish and vertical line total catch models, whereas only a single cyclic term was significant for the Red Grouper and bottom longline total catch models. Comparing each GAM with its corresponding periodic regression GLM using AIC, the GAM offered a superior fit, with the following exceptions: (1) the model fits were approximately equal (difference < 2) for the bottom longline Red Grouper catch and bottom longline total catch; and (2) the fit was only marginally better (difference < 3) for the bottom longline Tilefish catch.

The GLM results for Red Grouper catch and total catch in bottom longline gear were consistent with the GAM results, with peak CPUE predicted near the new moon and lower CPUE predicted near the full moon following a cosine function (Figure 5). The predicted effects on catch rates for Red Grouper captured with bottom longline gear were also similar

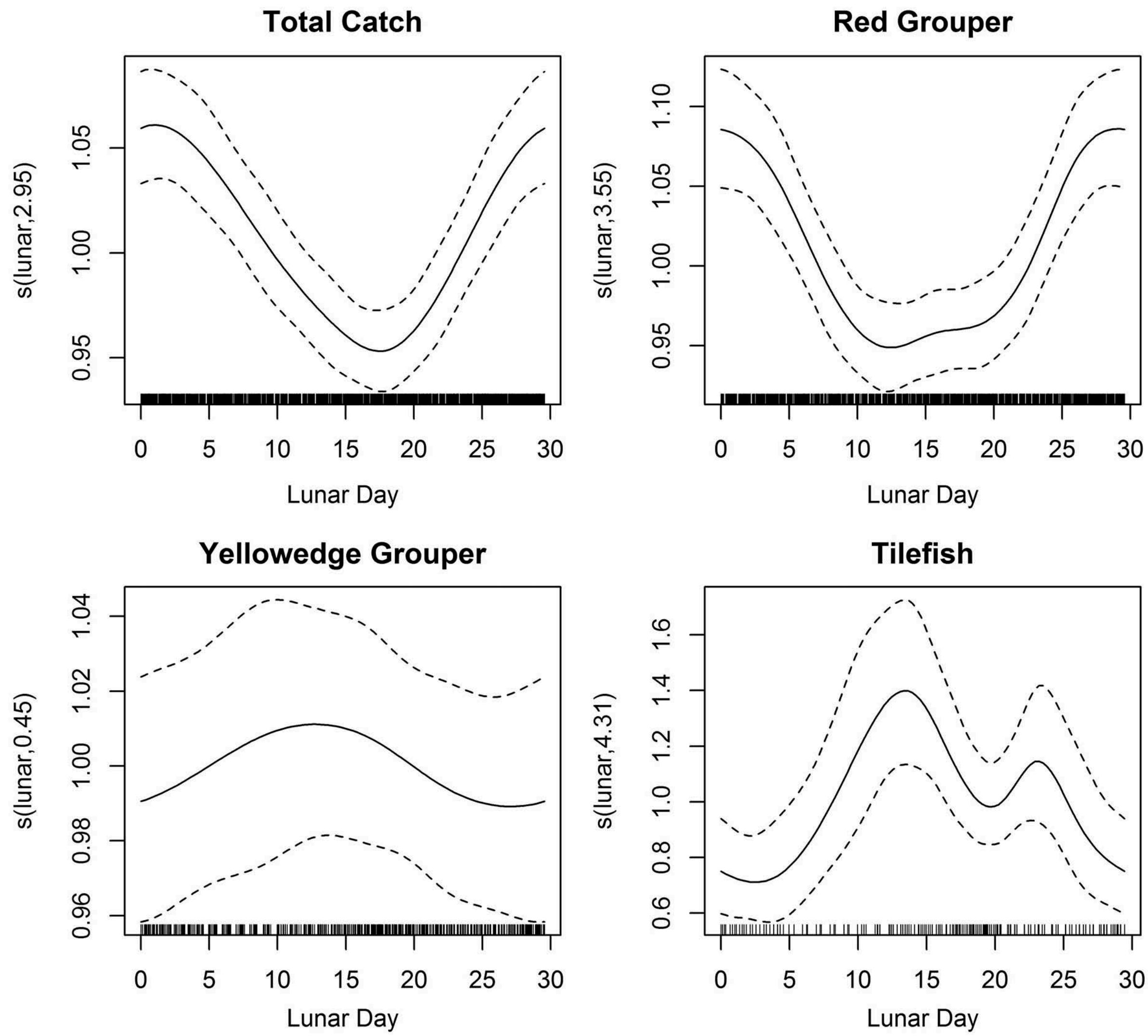

FIGURE 2. Smoothed curve (±95% confidence interval) of the additive lunar effect on predicted CPUE for bottom longline gear during the 29.5-d lunar cycle based on data from the commercial fishery for reef fish in the Gulf of Mexico. The ticks on the *x*-axis represent fishing sets during the lunar cycle used in the model. Each cyclic spline's estimated degrees of freedom are given on the *y*-axis label.

between methods, with approximately 1.1 times higher catch rates predicted to occur near the new moon. Tilefish results were consistent between methods, with catch rates predicted to increase near the full moon and during the waning moon phase. Likewise, each vertical line analysis was similar between models, as Red Grouper and total catch predictions from the GLMs were very similar to those predicted by the GAMs. The vertical line total catch and Red Grouper catch had similar predicted lunar effects, with increased CPUEs occurring near the waxing and waning lunar periods and a large decrease around the new moon, consistent with the GAM results. The GLM-predicted effect sizes for vertical line catch were slightly less than the effect sizes of each corresponding GAM. The periodic regression GLM diagnostics suggested acceptable levels of fit, but models fitted to the bottom longline data generally fit better than models fitted to the vertical line data, similar to observations for the GAMs (Figure S.9).

This study was primarily focused on the lunar effect, but the results of the other covariates may be of interest to other researchers. The change in the year effect from inclusion of the lunar information when it was significant resulted in only slightly different predicted changes in each model except for the Tilefish model, in which it had a greater effect (Figures S.10–S.11). For the bottom longline fishery, months in the first half of the year overall had much higher predicted catch rates for Red Grouper than months in the second half of each year. Tilefish captured in the bottom longline fishery also exhibited a strong trend wherein much lower catch rates were predicted during the summer months, especially in comparison with

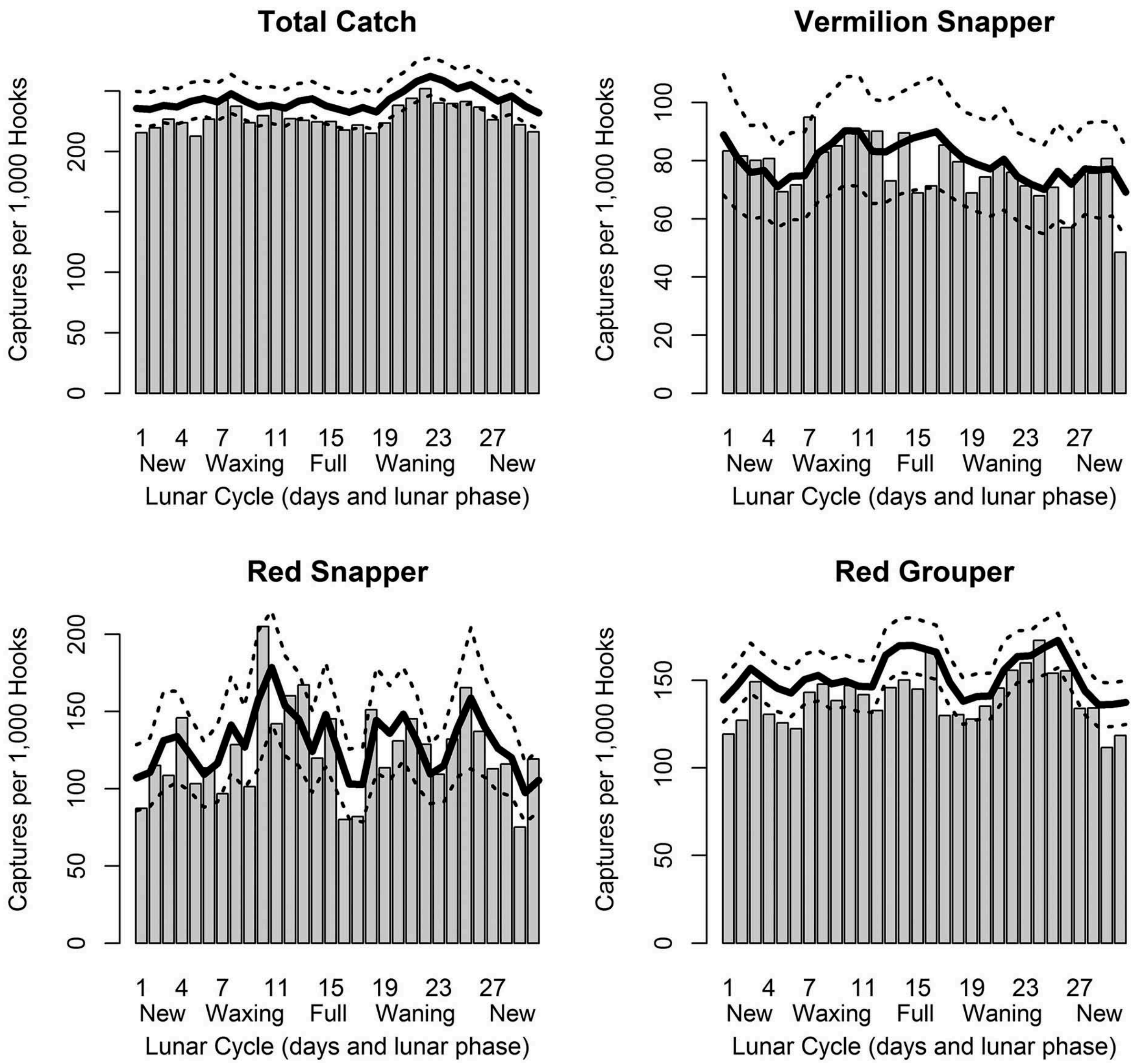

FIGURE 3. Bar plot of the mean observed CPUEs for each day in the 29.5-d lunar cycle compared with the CPUEs predicted by generalized additive models (solid line; ±95% confidence interval) for the three most common species and total catch with vertical line gear based on data from the commercial fishery for reef fish in the Gulf of Mexico.

Yellowedge Grouper, which only had slight deviations in predicted catch rates (i.e., a few lower catches during the winter months). In the vertical line fishery, no distinct pattern of change in catch rates across months was evident. Catch rates were predicted to be highest either in the morning or at midday for all analyses; the exception was Vermilion Snapper, for which the largest catch rates were predicted to occur at night, followed by evening.

DISCUSSION

I could find no anecdotal evidence that commercial reef fishers believe the lunar cycle affects catch rates, but the lunar cycle did significantly affect catch rates for some of the commercial reef fish species in the Gulf during the study. However, the largest observed magnitude of the predicted effect on catch rates was less than 40% for any analysis and was between 5% and 10% in most models. The most consistent pattern of lunar influence on CPUE from all modeling approaches was for Red Grouper captured in the bottom longline fishery, with CPUE predicted to increase around the new moon and to decrease proximal to the full moon following a cosine function. For aggregated total catch from bottom longline gear, the predicted changes in CPUE with the lunar cycle were similar to those for Red Grouper, but such similarities were expected because Red Grouper dominated the number of observed bottom longline captures (65%) and were targeted on the greatest number of fishing sets (78%). Tilefish captured

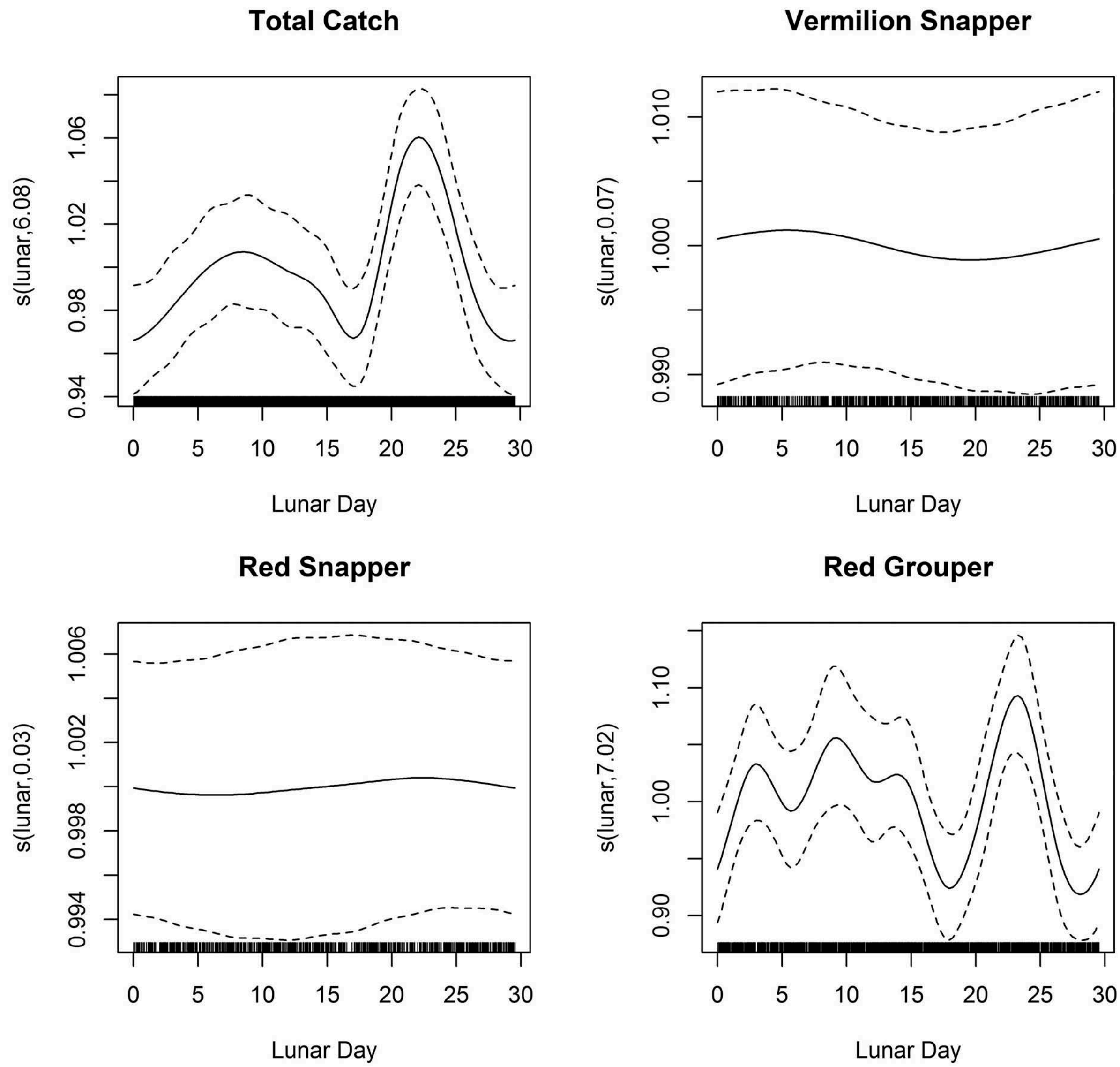

FIGURE 4. Smoothed curve (±95% confidence interval) of the additive lunar effect on predicted CPUE for vertical line gear during the 29.5-d lunar cycle based on data from the commercial fishery for reef fish in the Gulf of Mexico. The ticks on the *x*-axis represent fishing sets during the lunar cycle used in the model. Each cyclic spline's estimated degrees of freedom are given on the *y*-axis label.

with the bottom longline gear displayed contrary results: the largest increase in CPUE was predicted to take place before the full moon, and the lowest CPUE was predicted to occur near the new moon. The differences may be due to Tilefish being targeted on a much smaller number of fishing sets (<9%) than Red Grouper, thereby making the detection of a lunar effect more difficult; alternatively, the lunar mechanisms affecting CPUE may differ between species. The Yellowedge Grouper was the only bottom longline species for which the lunar cycle had no significant predicted effect in each of the models. One possible reason for the absence of a detected lunar effect on Yellowedge Grouper is that this species had the lowest observed catch rate of any targeted species (mean of ~20 captures per 1,000 hooks fished), thus making any small differences over the lunar cycle practically undetectable. For instance, a 5% increase in catch rate for Yellowedge Grouper would only result in approximately one more capture per 1,000 hooks fished, whereas in Red Grouper, a 5% increase would result in about four additional captures.

The species captured in the vertical line fishery had very consistent predicted changes in CPUE with each modeling approach. Red Grouper catch and total catch with vertical line gear had similar bimodal peaks, with CPUE predicted to increase near the waning and waxing lunar phases and the lowest CPUE predicted to occur near the new moon and full moon. Although the lowest nominal CPUEs for both

TABLE 3. Periodic regression generalized linear model (GLM) results (using backward regression) for the three most common species and total catch from each gear type in the commercial fishery for reef fish in the Gulf of Mexico. The final cyclic terms with coefficients, 95% confidence limits (LCL = lower confidence limit; UCL = upper confidence limit), and χ^2 *P*-values are reported for each model. The final column represents the difference in Akaike's information criterion (ΔAIC) between each final periodic regression GLM and its corresponding generalized additive model (GAM).

Species	Cyclic term	Coefficient	LCL	UCL	χ^2 *P*-value	ΔAIC (GAM – GLM)
		Bottom longline				
Red Grouper	Cosine θ	1.073	1.050	1.097	<0.001	1.26
Yellowedge Grouper	—	—	—	—	—	—
Tilefish	Cosine θ	0.728	0.628	0.843	<0.001	–2.81
	Sine 2θ	0.827	0.722	0.946	0.006	
Total catch (all species)	Cosine θ	1.054	1.035	1.074	<0.001	–1.08
		Vertical line				
Vermilion Snapper[a]	—	—	—	—	—	—
Red Snapper	—	—	—	—	—	—
Red Grouper	Cosine 2θ	0.964	0.940	0.988	0.004	–19.94
Total catch (all species)	Sine θ	0.987	0.974	0.999	0.049	–6.5
	Cosine 2θ	0.968	0.955	0.980	<0.001	

[a] The periodic regression GLM results for Vermilion Snapper were not included since the model failed to converge.

Vermilion Snapper and Red Snapper were observed near the new moon and, for Red Snapper, also proximal to the full moon, no lunar effect was detected with either modeling approach (Figure 3). One reason the lunar effect may have not been detected for the snapper species captured with vertical line gear is the difference in sampling methodology. Observers on vertical line vessels targeting Vermilion Snapper and Red Snapper typically do not sample the entire catch during each fishing set (NMFS 2016). Instead, they only sample a subset of all reels being fished during a set because each reel has between 15 and 40 hooks apiece. Conversely, vessels targeting Red Grouper with vertical line gear typically use 1–2 hooks per reel, and the entire catch is usually sampled. These gear differences result in Red Grouper having a much lower number of sampled fish captured per fishing set (3.2 sampled fish/set) compared to both snapper species, which had over 10.5 sampled fish captured per set. Additionally, increased variance in CPUE may be introduced through subsampling of fishing reels due to differences in efficiency among individual fishers on the vessel for fishing sets targeting snapper species. One possible method to reduce variation between gear types in future studies would be to summarize catch rates per day to minimize intraday variation in CPUE not directly related to the lunar cycle. Summarizing catch rates per day may allow for a more accurate comparison of CPUE between species, especially for Red Grouper vertical line data, in which more than 30 fishing sets per day are possible. Catch rates per day were not summarized for this data set because some fishers moved over a large geographic area during the same day, so the summarization of catch rates would have required either eliminating or summarizing some of the random covariates used in the study.

The inconsistencies in how lunar activity affects CPUE between different species in the same fishery were expected based on earlier studies. Poisson et al. (2010) found interspecific variation in the same fishery when examining lunar effects on Swordfish and Albacore CPUEs, and the differences were comparable to those observed between species in the present study. The largest inconsistency in predicted lunar effect in this study was between gear types for Red Grouper. These differences in predicted CPUE between gear types may be due to lunar activity affecting fishing efficiency in different ways. In his Solunar theory, John Knight proposed that the lunar cycle causes increased catch rates due to changes in fish behavior during specific times. From his observations, he proposed that increased activity and more aggressive feeding would occur around the new moon. The predicted increase in catch rates observed for the bottom longline fishery during the new moon was consistent with the Solunar theory. Many reef fish species, including groupers and Tilefish, are sedentary feeders with distinct territories for ambushing their prey (Thompson and Munro 1978); therefore, it is natural to conclude that increased activity would increase the probability of capture when a baited hook is offered. Another theory (proposed by Stevenson and Millar 2013) is that the reduced illumination near the new moon hinders feeding at night since the ability to spot prey is decreased in comparison with nights when higher lunar illumination is present. The decreased feeding at night results in hungrier, more aggressive fish around the new moon, thus increasing their catchability.

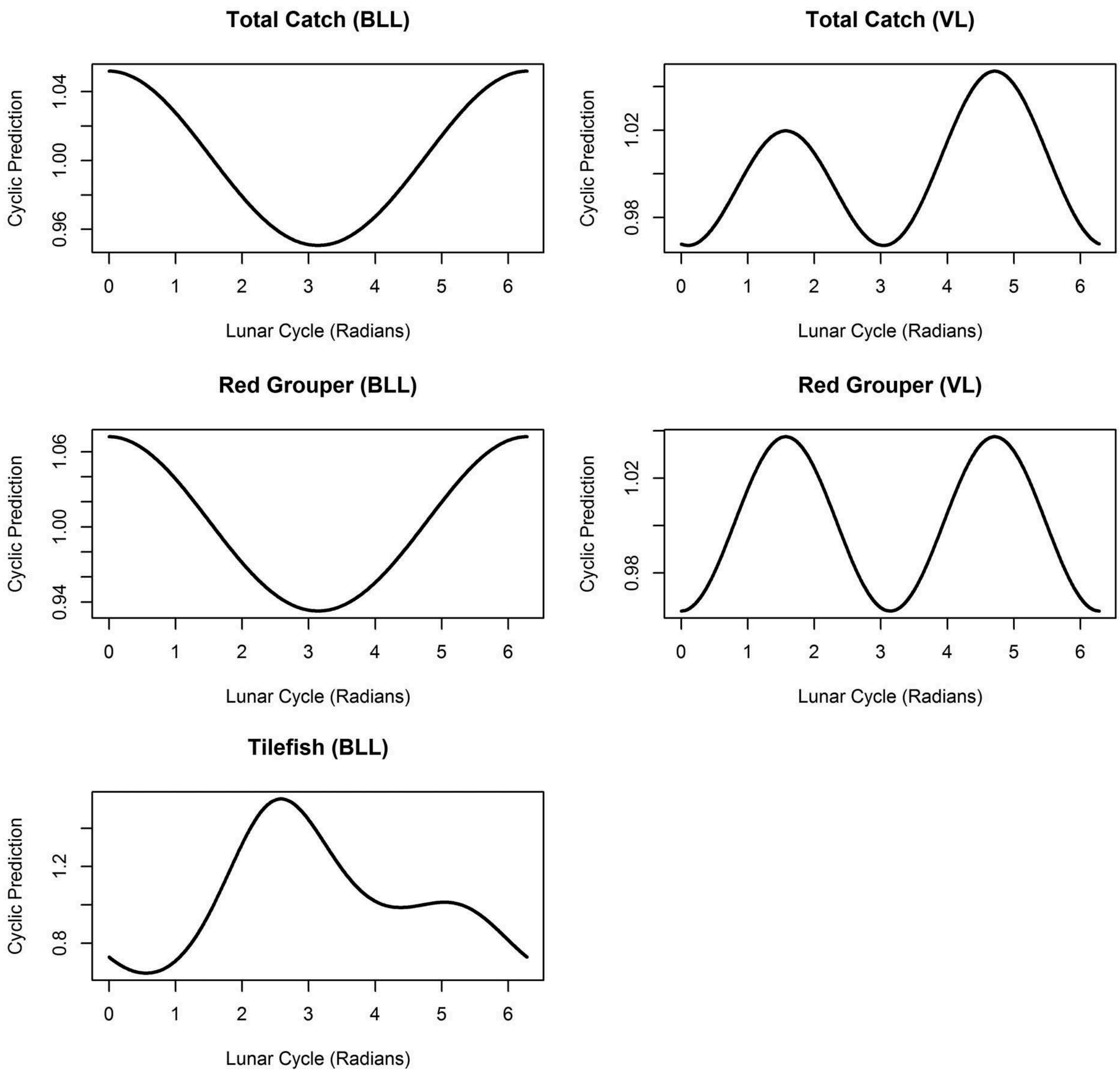

FIGURE 5. Significant cyclic (sine or cosine) lunar effects on predicted CPUE for the lunar month (in radians) for bottom longline (BLL) and vertical line (VL) gear types in the commercial fishery for reef fish in the Gulf of Mexico.

The theory hypothesizing diminished feeding at night may also explain why an increase in Tilefish CPUE was not predicted near the new moon. On average, Tilefish are captured at much greater depths than Red Grouper (248 versus 45 m), and at these deeper depths, differences in lunar illumination may be less important than other sensory mechanisms of food detection by Tilefish.

For vertical line gear, a different mechanism unrelated to fish behavior might be causing the predicted changes, as the majority of species had minimum CPUEs predicted near the new moon—the period when greater fish activity should be likely based on either of the previously discussed theories. Vertical line vessels typically fish by anchoring at a number of locations that are believed to contain target reef fish species. If few or no target species are captured, the vessel will likely change to a more desirable location or alter its fishing practices. It is hypothesized that since stronger tides occur near the new and full moons (spring tides), the ability of vertical line fishers to accurately anchor or drop a baited hook to fishing depth at a location is impeded, accounting for the reduced CPUE during those times. The potential reduction in vertical line gear efficiency caused by increased tidal strength could reduce any increase in catch rate obtained through more aggressive feeding behavior. Conversely, periods of lesser tidal strength occurring near the quarter moons (neap tides) should increase the efficiency of vertical line fishers in anchoring and presenting bait. An increase in CPUE during the waxing or waning lunar phase was predicted for Red

Grouper and total catch on vertical line gear, consistent with the proposed change in gear efficiency. Additionally, when fishing is poor, other factors may account for differences between gear types. In comparison with bottom longline vessels, vertical line vessels are able to quickly alter their routine by changing locations, fishing duration, bait types, or target species, possibly confounding the detection of the lunar effect on fish behavior. The increased vertical line efficiency was also evident when the capture rates of a given species were compared between gear types. Bottom longline gear was typically much less efficient than vertical line gear at capturing Red Grouper: the number of Red Grouper captured per 1,000 hooks was about 75 for bottom longlines but approximately 150 for vertical line gear. Although the Solunar theory remains unconfirmed for the fishery because solar and daily tidal activity could not be included in the study, the bottom longline results were consistent with the theory, predicting increased catch rates around the new moon.

In addition to the year, month, area, time of day, and depth effects examined here, future research may benefit from the inclusion of other environmental covariates that were unavailable for this study, such as barometric pressure or water temperature. Hanson et al. (2008) found that lunar activity influenced the activities of Largemouth Bass *Micropterus salmoides*, but the patterns were not consistent across seasons. Vinson and Angradi (2014) found that elevated CPUEs for Muskellunge were closely correlated with a cosine 2θ function, showing peaks near the new moon and full moon; however, the effect varied greatly with latitude and by month. Although it is theorized that latitude would have a minimal effect in a fishery for subtropical reef fish, seasonal variations may have a tremendous impact, especially if they coincide with differences in the reproductive cycle. The lunar cycle has been known to coincide with spawning aggregations for numerous reef fish species, such as the Cubera Snapper *Lutjanus cyanopterus*, during the new moon (Takemura et al. 2004; Heyman et al. 2005). Spawning aggregations are often targeted by fishers due to increased catchability, and for certain hermaphroditic grouper species in the Gulf, overfishing has occurred, with serious long-term management consequences such as highly skewed population sex ratios (Coleman et al. 1996). Although seasonal variations likely have greater effects on fish behavior in colder climates than in the Gulf, the extent of the difference is unknown. In addition, research on the efficiency of baited fishing gear should also focus on other factors not available for this study, such as bait type and hook size selectivity. Belcher and Jennings (2009) evaluated sources of bias in a bottom longline survey program focused on coastal sharks; those authors found no lunar or tidal effect, but they did detect significant differences in shark catch rates between two bait types.

As indicated by the diagnostic plots, models that were fitted to bottom longline catch data provided an overall better fit than models that were fitted to vertical line data. The differences in fit were most likely due to higher percentages of zero catch recorded for vertical line gear; a large percentage (41%) of zero catches was recorded for vertical line vessels targeting Red Grouper. Future studies may benefit by comparing the negative binomial distribution to the different zero-inflated approaches available. Walsh and Brodziak (2014) standardized billfish CPUEs using observer data with five different types of GLM and found that a zero-inflated negative binomial approach was the most appropriate for a number of species, as it accounted for both the zero inflation and the overdispersion present in positive catch data. Gray (2005) found that the negative binomial and the zero-inflated negative binomial models were superior for modeling similar problematic count data in comparison with Poisson, zero-inflated Poisson, log-transformed, or square-root-transformed models. The study by Gray (2005) also emphasized that a negative binomial model could perform as well or better without a zero-inflated component depending on the process of zero generation in the data set. Another possible future research choice that has outperformed a negative binomial model is the hurdle model, which assumes that all zero observations are true negatives, whereas zero-inflated models attempt to differentiate between the zero-generating processes (Potts and Elith 2006). Due to the inherent nonlinearity associated with the lunar cycle, GAMs and periodic regression GLMs were preferred for modeling the lunar effect. Although periodic regression represents a parsimonious and perhaps more interpretable alternative to GAMs for exploring lunar effects on catch data, the GAM is recommended due to the number of distributional choices available and the flexibility in fitting multiple nonlinear covariates that may not be cyclic. When interpreting the GAM, inference should be limited to overall trends, and caution should be used when interpreting small changes in amplitude (“wiggliness”) resulting from other factors not related to the covariate of interest.

The lunar cycle affects catch rates for some reef fishes, but the lunar influence is not limited to species of finfish captured with baited hooks. Other studies have determined that the lunar cycle influences catch rates for trawl and trap gears targeting commercially important lobster, shrimp, and squid species (Chiou et al. 2003; Srisurichan et al. 2005; Masuda et al. 2014). The methodology outlined in this study for detecting a lunar effect will be beneficial to other researchers interested in correlating environmental factors that have been shown to influence CPUE. Relative abundance indices used to detect long-term trends based on nominal CPUE can be problematic due to a number of confounding variables influencing catch rates (Maunder et al. 2006). Most commonly, CPUE is standardized to compensate for some of these factors to provide a relative abundance index for measuring population status (Maunder and Punt 2004). Ideally, standardized indices of abundance should use nominal CPUEs derived from fishery-independent surveys with adequate temporal and spatial coverage;

however, these ideal coverage levels are often impractical due to funding limitations and/or survey design. Fishery-dependent data sets are therefore frequently relied upon to provide CPUEs for indices of abundance, but those data sets can be suspect due to changes in fleet efficiency, gear selectivity, and altered targeting practices by fishers (Maunder et al. 2006). Current methods for standardizing CPUE data often include environmental conditions that are believed to influence catchability, such as water temperature and large-scale oceanic conditions (e.g., El Niño or red tides). A review by Stoner (2004) on the effects of environmental factors, including water temperature, light levels, and current velocity, found that these factors could potentially influence CPUE by a factor of 10. Although the lunar effect was mostly small for the species examined in this study, differences were present in the confidence intervals comparing the term plots for the year effect when the lunar spline was removed from the models.

Since stock assessments assume that catchability is proportional to overall population abundance, it is critical to develop a greater understanding of factors shown to influence catchability. When catchability parameters were integrated into an assessment model for the Red Grouper fishery near the Campeche Bank in Mexico, Arreguín-Sánchez (1996) concluded that clear differences in abundance estimates were present when catchability effects were included. Arreguín-Sánchez (1996) determined that Red Grouper catchability was strongly influenced by reproductive behavior, age structure, and different months of the year. The most recent stock assessments for the species in this research have not relied on standardized indices of abundance derived from fishery observer data, most likely due to the short time period of such data in comparison with historical self-reported coastal logbook data and fishery-independent surveys in the region. Nevertheless, it is anticipated that fishery observer data will likely be utilized more in the Gulf region as the time series expands and because observer data are typically considered more reliable than self-reported data. When Walsh and Brodziak (2014) standardized billfish CPUEs by using observer data in the Pacific, they determined that lunar illumination was a significant variable in the final models for three of the four billfish species examined. Based on the present study, lunar information will likely improve the fit of standardized indices of abundance using fishery-independent or fishery-dependent data sources for some reef fish species in the Gulf. In conclusion, this research aims to contribute to a greater understanding of the lunar cycle's effects on catch rates and possibly to reduce uncertainty in some of the estimates, thereby benefiting the long-term management goals of the fishery.

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